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Valve sculpturing and aesthete distributions in four species of Australian chitons (Mollusca: Polyplacophora)

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ABSTRACT

The shell valve surfaces of the chitons *Ischnochiton (Ischnoradsia) australis*, *Cryptoplax mystica*, *Liolophura (Liolophura) gaimardi* and *Onithochiton quercinus* are studied by scanning electron microscopy. The distribution of aesthete caps is examined in relation to dorsal sculpturing, and the formation of these complexes is compared with the arrangement of holes which penetrate the ventral surface and eave tissue. The presence of specialized aesthetes (ocelli) on *Liolophura (L.) gaimardi* and *O. quercinus* is described. The use of aesthete densities as taxonomic indicators, and possible functions in relation to species specific environmental conditions are discussed.

INTRODUCTION

The Polyplacophora are unique among molluscs - having a highly complex shell structure penetrated in the tegmentum by numerous aesthete channels. Proximally these channels terminate in apical and subsidiary caps, visible under the light microscope as circular/oval apertures. Scanning electron microscope (SEM) investigations have been conducted on a limited number of species (Boyle, 1976; Haas, 1972, 1977; Haas & Kriesten, 1978; Fischer & Renner, 1979; Baxter & Jones, 1981, 1984; Baxter, Jones & Sturrock, 1987) and have contributed to our knowledge of both the function and distribution of these aesthete structures. It is clear that the arrangement of apical, and to a lesser degree subsidiary caps is of systematic importance. Recent phylogenetic studies (Leloup, 1974; O'Neill, 1985; Bullock, 1985) have employed apical cap densities as useful taxonomic indicators.

This paper presents the first detailed observations of both the gross and the fine morphology of the shell valves on four species of Australian chitons: *Ischnochiton (I.) australis* (Sowerby, 1840), *Cryptoplax mystica* Iredale & Hull, 1925; *Onithochiton quercinus* (Gould, 1846) and *Liolophura (L.) gaimardi* (De Blainville, 1825). All species are common inhabitants of the intertidal zone on the New South Wales coast, the two former species being largely confined to the

bottom of the littoral zone in sheltered areas, and the latter being restricted to open surfaces on exposed headlands. The distribution of aesthete complexes is examined, and their possible use as taxonomic indicators, and their function in relation to habitat are discussed.

MATERIALS AND METHODS

Specimens of the chitons *Ischnochiton (I.) australis*, *Cryptoplax mystica*, *Liolophura (L.) gaimardi* and *Onithochiton quercinus* were collected from rocks in the intertidal region at Arrawarra on the mid north coast of New South Wales (30°10'S, 15°20'E).

After narcotization in 10% $MgCl_2$, $6H_20$ solution in sea-water, the shell valves were carefully removed from the animal. Material to be used for light microscopy was fixed in 7% formaldehyde solution, washed in distilled water, and decalcified in 5% disodium ethylenediaminetetraacetic acid (EDTA). Small sections of valve were then examined on a Kyowa UNILUX-12 phase contrast microscope. Valves for scanning electron microscopy were treated as follows. After washing in distilled water, a number of valves were ultrasonically cleaned and air-dried as a control. The remaining material was treated with a 5% solution of KOH for 24 hours to remove organic material, and then rinsed in distilled water, ultrasonically cleaned and air-dried or dehydrated in an alcohol series (Baxter and Jones, 1984). Specimens were subsequently mounted with colloidal copper on aluminium stubs, sputter-coated with gold, and examined at an accelerating voltage of 20 kV on a JOEL JSM35 scanning electron microscope. For line drawings, uneroded valves were taken from juvenile individuals also used for SEM studies. These valves were mounted on pins and coated with magnesium oxide in order to enhance sculptural detail (Bullock, 1985).

The species names and systematic classification used in this paper are taken from Kaas & Van Belle (1980). The morphological nomenclature and shell valve numbering are those of Baxter & Jones (1981).

RESULTS

Valve morphology of *Ischnochiton (I.) australis* (Ischnochitonidae)

The anterior valve (I) has twenty to thirty irregular ribs diverging towards the margin (Fig. 1(a)). The tegmentum is comparatively smooth and the small rounded apical caps (mean maximum diameter (mmd) 11.3μm ± 0.3μm, n=38) appear to be evenly distributed throughout the shell surface. Associated subsidiary caps are much smaller (mmd 5.0μm ± 0.2μm, n=28) and are distributed randomly around these apical caps.

Unlike valve (I), the intermediate valves of *I.(I.) australis* (Fig. I(b)) have distinct regions, similar to those shown by Baxter & Jones (1984) for *Callochiton achatinus* (Brown, 1827). The lateral areas have four to six diverging ribs (extending throughout a surface without papillae); the median areas in comparison display regular rows of slightly raised papillae. Towards the jugum these papillae become weak, eventually fusing to leave small concave depressions (approximately 40μm in length) in the shell surface (Fig. 2). As a result of the distinct variation in gross valve morphology, the distribution of apical and subsidiary caps in these areas varies considerably (Table I): in the median/jugal areas the occurrence of apical

caps is limited to the raised papillae, although some subsidiary caps are located in the concave depressions; the shell surface of the lateral area is covered with regular rows of subsidiary caps connected by shallow grooves and interspersed with apical caps (Fig. 3). The absence of papillae, in this area, results in a much higher density of both apical and subsidiary caps. The number of subsidiary caps associated with each apical cap, however, appears to remain similar to that for the jugal area.

The sculpturing on the central area of the posterior valve (VIII) is analogous to the jugal region of the intermediate valves (Fig. I(c)). Small flattened papillae fuse, leaving a shell surface indented by shallow pits. In this region the apical caps are restricted, as in intermediate valves, to the dorsal surface of the raised papillae, and are arranged on grooved lines linking adjacent subsidiary caps. Postmucronal, the gross sculpturing is similar to that found on the anterior valve. The ribs, however, tend to be more irregular and nodulose as a result of growth interruption lines. Here the subsidiary caps are evident, and arranged in parallel rows linked by shallow grooves. These grooves are interrupted only by growth lines and apical caps.

It is apparent that similarities in the gross structure of the antemucronal area in valve (VIII), and the jugal region of intermediate valves, are not reflected in the distribution of aesthetes. A comparison of apical and subsidiary cap densities (Table I) indicates that shell tissue in the posterior valve is penetrated by approximately twice as many aesthete complexes as in intermediate valves. The number of subsidiary caps associated with each apical cap does, however, remain relatively constant. Although the postmucronal area of valve (VIII) and the anterior valve have similar gross sculpturings and the respective apical cap densities compare well, the number of subsidiary caps per mm^2 in valve (VIII) is almost half that recorded for valve (I). Consequently the ratio of apical to subsidiary caps is smaller.

The ventral surface is perforated by numerous channels. In valve (I) these perforations occur in three distinct areas; along the lateral portion of the posterior edge, in the central area (midway between the anterior and posterior edges), and in narrow slit rays radiating from the central posterior edge to interruptions between adjacent insertion teeth. In this latter class, 20-25 such rays were observed in those specimens examined. Between these slit rays in the central area, the articulamentum is cancellated with numerous slit-like fissures arranged transversely (Fig. 4). This type of structure is not present on the posterior edge. In this region channel openings are small, rounded and dispersed randomly.

The organization of aesthete channel openings on the ventral surface of intermediate valves is different to that of the anterior valve. The posterior lateral edge is not perforated, and the number of slit rays present is much reduced (2-4 occurring on those individuals examined). Additionally, the jugal area is penetrated by large numbers of elliptical holes opening onto narrow fissures, which often interconnect and extend beyond the jugal area.

In valve (VIII) the posterior region is not perforated by rounded apertures. With this exception, the ventral surface is similar to that of valve (I), with 20-30 slit rays diverging from the mucro, and an antemucronal area penetrated by slit fissures.

In addition to those channels which perforate the ventral surface, many holes penetrate the eave tissue along the lateral and anterior edges of valves (I-VII) (Fig. 5), and throughout the circumference of valve (VIII). These correspond with the

growing edges of the different shell valves, and hence the formation of aesthete complexes. The development of these aesthete structures can be deduced through observations of various stages of construction along the exposed margins. In *I. (I.) australis* (Fig. 6) interruptions on the growing edge to form shallow depressions are followed by narrow fissures running to and from this structure. As new material is deposited on the periphery of the indentation a large channel is formed and fissures linking this to the dorsal surface eventually become encircled, giving rise to apical and subsidiary ducts. On the further addition of material to the growing edge the channel aperture becomes disposed ventrally, indicating an increase in the width of the eave tissue with increasing age.

Valve morphology of *Cryptoplax mystica* (Cryptoplacidae)

The anterior valve exhibits diverging nodulose sculpturing (Fig. 1(d)). Apical caps are confined to the central region of these nodules where they occur in an evenly spaced single row (Fig. 7). The density of these apical caps is low compared with the other species studied (Table 1), while the number of indistinct subsidiary caps cannot be sufficiently accurately determined. The ratio of subsidiary to apical caps is probably rather large, as indicated by the occurrence of subsidiary caps in certain internodulose areas and especially on the lateral and anterior edges.

The jugal area of the intermediate valves is smooth with weak crescentic ribbing (Fig. 1(e)). The lateral triangles, in contrast, are distinctly nodulose, with longitudinal rows of nodules radiating from the posterior. Apical caps in the jugal region are rounded (mmd 11.4μm ± 0.2μm, n=22), and like valve (I), occur in low numbers (Table 1) and are allied with an undetermined number of indistinct subsidiary caps. Apical caps in the lateral triangles are restricted to the large raised papillae and do not occur either on the edges or between these structures; hence the density of apical caps in these lateral triangles is very low (48 apical caps/ mm^2).

Like the intermediate valves, the posterior valve has a smooth lightly ribbed jugal area, while the median areas exhibit a sculpturing of nodulose processes arranged in rows radiating from the terminal mucro. The apical caps found in the jugal area are elliptical in shape (mmd 11.1μm ± 0.4 m, n=42), and are more numerous on valve (VIII), than in any preceeding valves (Table 1). For the material examined, subsidiary caps were distinguishable on the posterior valve surface, unlike that for the head and intermediate valves, and were found to occur at a density of 868 caps/ mm^2 giving a ratio of 2.7 subsidiary caps for each apical cap. In the median areas, the apical cap density is relatively much reduced resulting from their distribution being limited to the dorsal surface of raised oval papillae (Fig. 8). Subsidiary caps were again largely concealed; however, some subsidiary caps were noted to occur both on the papillae and in the troughs of adjacent papilla in the median region. On the ventral surface of valve (I), the insertion plates are thrown abruptly forward and flattened. The aritculamentum does possess some apertures, antero-posteriorly and deep irregular fissures running anteroposteriorly, however slit rays are absent. In comparison, the ventral surface of the intermediate and posterior valves is highly perforated (Fig. 9), with numerous channel openings in the jugal area becoming fewer towards the posterior edge. These valves also possess small crystalline processes in the posterior lateral fields (Fig. 10). The toroid structures do not appear to be apertures, but merely extensions of the hypostracum.

Table 1. Size and density of apical and subsidiary caps. Mean maximum diameters are given in micrometres ± S.D. for (n) number of caps measured. Density is defined as number of caps per mm^2

Region	*Species*	*Apical Diam.*	*Sub. Diam.*	*Apical Density*	*Sub. Density*	*Ratio*
Valve I						
Central	I. australis	11.3±0.3,n=38	5.0±0.2,n=28	405	1600	1:3.9
	C. mystica	13.2±0.4,n=35	5.2±0.3,n=12	114		
	L. gaimardi	8.3±0.1,n=28	3.4±0.3,n=25	257	7247	1:28.0
	O. quercinus	9.5±0.3,n=44	4.2±0.1,n=18	650	11100	1:17.1
Valve IV						
Jugal	I. australis	10.5±0.4,n=48	5.1±0.1,n=20	288	867	1:3.0
	C. mystica	11.4±0.2,n=22		107		
	L. gaimardi	10.9±0.4,n=43	3.8±0.2,n=38	104	3500	1:33.7
	O. quercinus	9.4±0.1,n=35	4.7±0.2,n=40	234	8100	1:34.6
Lateral	I. australis	14.0±0.4,n=45	5.4±0.3,n=33	425	1825	1:4.3
	C. mystica	9.8±0.1,n=24		48		
	L. gaimardi	11.5±0.6,n=34	3.7±0.2,n=28	166	5900	1:35.5
	O. quercinus	9.3±0.2,n=15	4.3±0.1,n=26	376	6300	1:16.8
Valve VIII						
Premucral	I. australis	8.9±0.5,n=36	4.5±0.4,n=47	537	2040	1:3.8
	L. gaimardi	10.0±0.5,n=40	3.9±0.2,n=30	162	4800	1:29.6
Postmucral	I. australis	9.9±0.3,n=25	4.8±0.2,n=30	396	936	1:2.4
	L. gaimardi					
Jugal	C. mystica	11.1±0.4,n=42	4.9±0.3,n=33	323	868	1:2.7
	O. quercinus	8.9±0.3,n=20	4.1±0.3,n=32	260	6500	1:25.0
Median	C. mystica	11.3±0.2,n=30		87		
	O. quercinus	8.8±0.1,n=17	4.0±0.2,n=18	228	5100	1:22.3

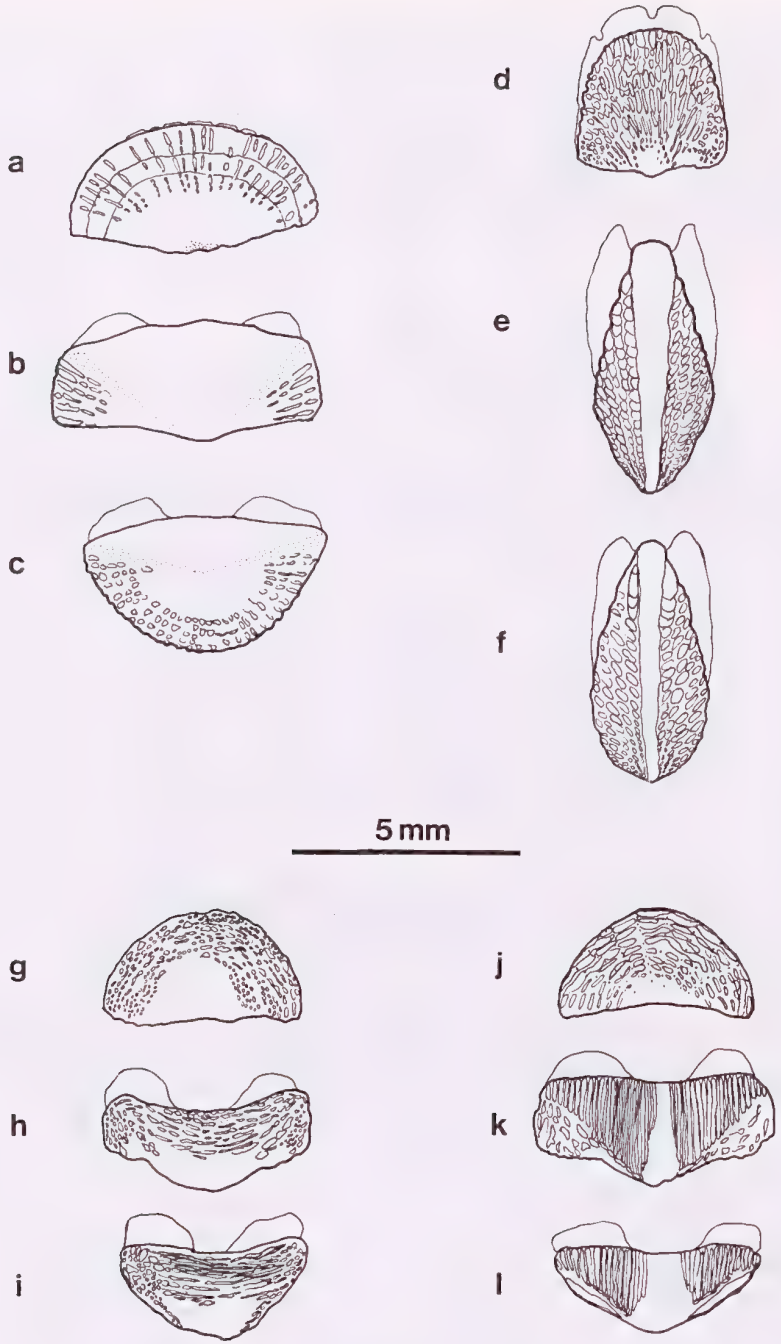


Figure 1. Dorsal valve sculpturing. a-c, *Ischnochiton (I.) australis*; d-f, *Cryptoplax mystica*; g-i *Liolophura (L.) gaimardi*; j-l *Onithochiton quercinus*. Anterior valve - top, intermediate valve -middle, posterior valve - bottom.

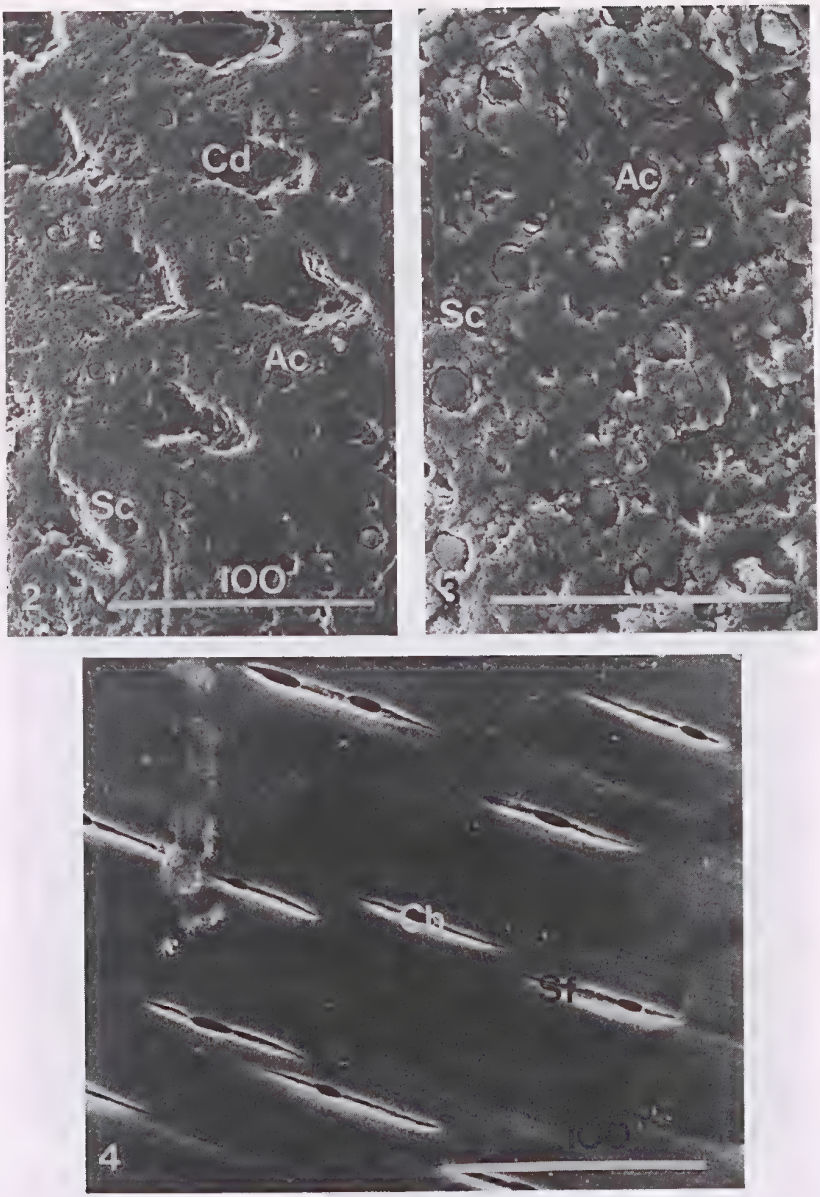


Figure 2. Shell surface of *I. (I.) australis* in the jugal area, showing the surface sculpture indented by shallow concave depressions (Cd), and the distribution of apical (Ac) and subsidiary (Sc) caps. Scale bar in micrometres.

Figure 3. Shell surface of *I. (I.) australis* in the lateral area, showing parallel rows of subsidiary caps (Sc) connected by shallow grooves, and with apical caps (Ac) disposed evenly along these. Scale bar in micrometres.

Figure 4. Ventral surface of the anterior valve of *I. (I.) australis* in the central area, showing elliptical aesthete channels (Ch) opening onto transversely-arranged slit fissures (Sf). Scale bar in micrometres.

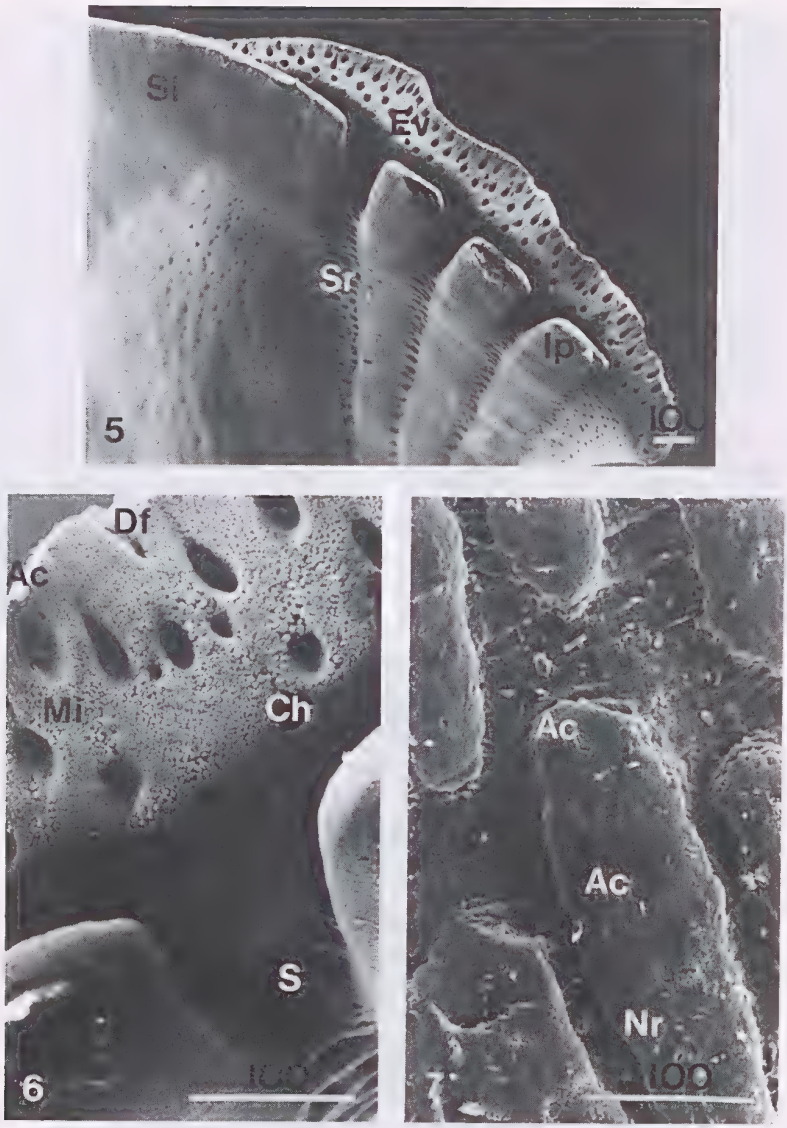


Figure 5. Intermediate valve of *I. (I.) australis* showing the distribution of aesthete channel openings throughout the eave tissue (Ev), and along slit-rays (Sr) running between adjacent insertion plates (Ip) and sutural lamina (Sl). Scale bar in micrometres.

Figure 6. The eave tissue on the lateral edge of an intermediate valve of *I. (I.) australis* in the region of a slit (S), showing megalaesthete channels (Ch) disposed ventrally, and the formation of a new aesthete complex, with micraesthete openings (Mi), near the dorsal surface. Duct fissures (Df) running to apical (Ac) and subsidiary caps from the aesthete complex eventually become encircled as new material is deposited, forming apical and subsidiary channels respectively. Scale bar in micrometres.

Figure 7. Dorsal surface of an anterior valve of *C. mystica* in the lateral area, showing the distribution of apical caps (Ac) along the nodulose ridges (Nr). Scale bar in micrometres.

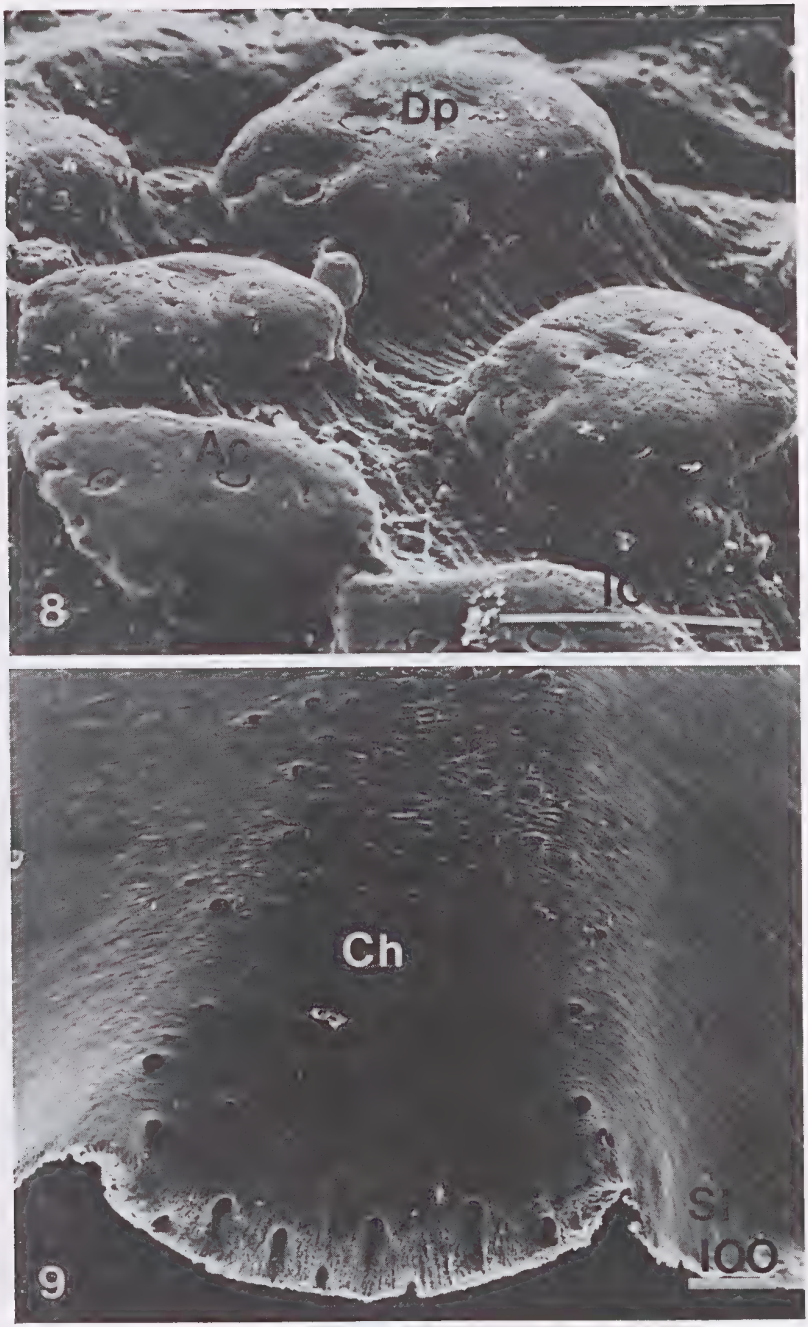


Figure 8. Raised dorsal papillae (Dp) and associated apical caps (Ac) on median area of an intermediate valve of *C. mystica*. Scale bar in micrometres.

Figure 9. Aesthete channel of openings (Ch) between sutural lamina (Sl), on the anterior ventral region of an intermediate valve of *C. mystica*. Scale bar in micrometres.

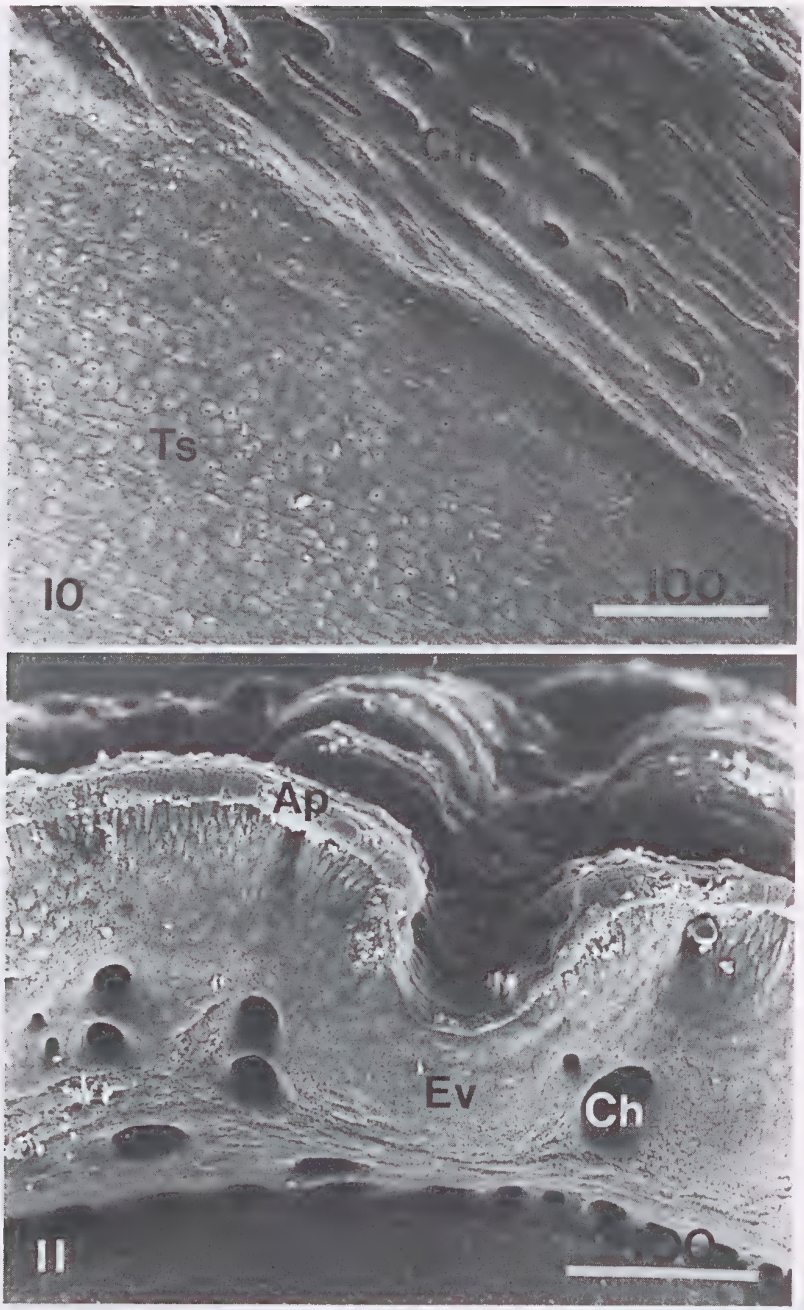


Figure 10. Ventral surface of an intermediate valve of *C. mystica*, showing toroid structures (Ts) extending from the hypostracum adjacent to aesthete channel openings (Ch) in the posterior lateral area. Scale bar in micrometres.

Figure 11. Eave tissue (Ev) on the lateral edge of the posterior valve of *C. mystica*, showing aesthete channel openings (Ch), and the formation of an apical channel (Ap). Scale bar in micrometres.

The eave tissues in *C. mystica* is perforated by aesthete channels in a similar fashion to *I.(I.) australis*, with the openings occurring on the lateral and anterior edges of valves (I-VII), and throughout the circumference of valve (VIII) (Fig. 11). Additionally, it appears that posterior infoldings on the ventral surface of intermediate valves undergo growth accompanying that in the lateral fields. Although the shell in this ventral area is not perforated with large holes as in the lateral area, the tissue is a continuum with the dorsal surface and shows clearly marked growth check lines on the non-papilliate surface. In valve (VIII) the eave tissue at the anterior edge does not seem to be associated with many aesthete channels, especially when related to the high number of apical caps on the dorsal jugal area. The aesthetes in this area cannot therefore be formed in the manner described for *I. (I.) australis,* and must be unbranched systems formed by fissures running dorso-ventrally throughout the four shell layers.

Valve morphology of *Liolophura (L.) gaimardi* (Chitonidae)

The sculpturing on all valves (Fig. 1(g-i)) displays concentric rows of raised papillae, becoming more pronounced towards the margins. In valve (I) a regular grid pattern of subsidiary caps (mmd 3.4μm ± 0.3μm, n=25) is evident over the entire dorsal surface, where it is uneroded (Fig. 12), at a density of 7247 subsidiary caps per mm^2. In comparison, apical caps (mmd 8.3μm ± 0.1 μ m, n=28) are restricted to the central area of the raised papillae with a density of 257 caps per mm^2, indicating that a relatively large average number (28) of subsidiary caps are in association with each individual apical cap.

The jugal area of the intermediate valves is sculptured, at a microscopic level, by a series of shallow grooves connecting adjacent subsidiary caps. These longitudinal grooves are continuous throughout the antero-posteriorly aligned nodes, intersected only by growth check lines and apical caps. The latter occur in transverse rows through the apex of the raised papillae. The lateral triangle is similarly arranged (Fig. 13); however, unlike the jugal area the grooves run transversely.

On the posterior valve, the concave postmucronal slope is generally largely eroded and hence sculpturing and the distribution of apical and subsidiary caps in this area is undetermined. In the antemucronal area, the nodulose ridges are rectangular in shape (Fig. 14), and subsidiary caps are arranged in a manner similar to that of valve (I). Likewise the apical caps are situated at subsidiary cap grid junctions, disposed in lateral rows extending through the apex of the raised papillae.

The valves of *L. (L.) gaimardi* also possess ocelli type structures similar to those described for *Schizochiton incisus* (Sowerby, 1841) by Moseley (1885). These ocelli appear as large (mmd 64.7μm ± 3.4μm, n=27) convex circular structures (Fig. 15) and are highly refractive when viewed at the light microscopic level. When decalcified they appear to be embedded in ovaloid regions of pigmented tissue (approximately 100μm diameter); their distribution varies between valves. They are particularly numerous on valve (I), occurring, in no apparent pattern, throughout the frontal margin. In proceeding shell valves, they are similarly disposed anteriorly towards the non-eroded growing edge.

Sculpturing of the ventral surface is limited. In valve (I), 9-11 crenulate insertion plates are arranged along the anterior and lateral edges. The surface is smooth and slit rays are absent. By comparison intermediate valves exhibit one pair of slit rays

originating from the central posterior edge and terminating at a notch between the anterior sutural lamina and lateral insertion plate. The eave tissue in valves (I-VII) is penetrated by aesthete channels on the anterior and lateral margins. In contrast valve (VIII) has an additional field of channel openings at the posterior. These are disposed ventrally and are consistent with an infolding of the growing edge. Elsewhere, the ventral surface is smooth and unsculptured.

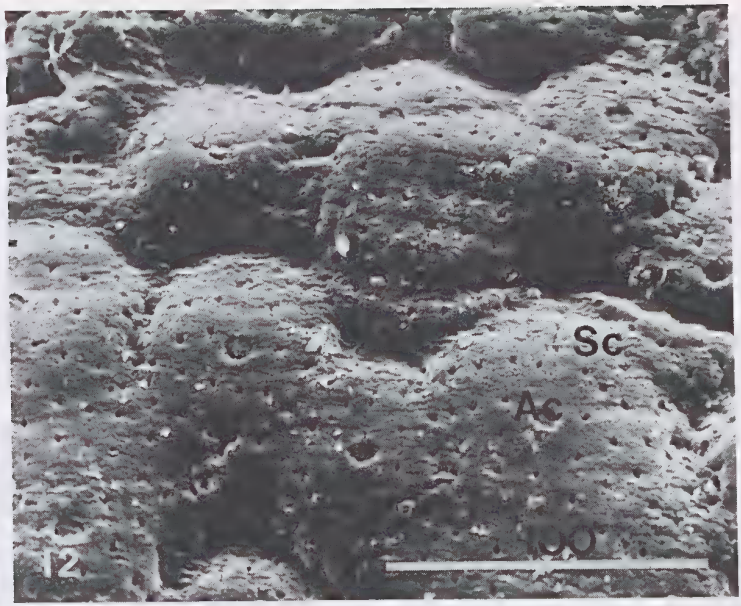
Valve morphology of *Onithochiton quercinus* (Chitonidae)

The anterior valve is sculptured with 8 or 9 radial rows of ocelli separated by a series of crescentic sulsi giving an appearance of imbricating flattened broad scales (Fig. 1(j). The ocelli (Fig. 16) are circular in shape (mmd 45.2μm ± 0.5μm, n=32), with a characteristic elliptical cap (approximately 5μm diameter) disposed towards the lateral edge. The number of these structures present was generally found to increase with shell size, even though a number are lost in older individuals by erosion. Subsidiary caps are very numerous and are arranged in lines connected by shallow grooves. The apical caps are disposed along these lines at regular intervals but are limited in proximity to ocelli. Large numbers of subsidiary caps are present immediately adjacent to the ocelli; apical caps however, although surrounding individual ocelli, do not occur within a 45μm (approximately) radius of the ocelli centre.

On the intermediate valves, the lateral areas are slightly raised and transected by diagonal ribs consisting of weak semi-nodulose structures. Longitudinal, wavy, closely set riblets cover the median areas, becoming weak towards the jugum (Fig. 1(k)). Apical caps in the central zone are not restricted to the apex of the longitudinal riblets, but are occasionally found in the troughs between these ribs (Fig. 17). These apical caps are circular (mmd 9.4μm ± 0.1μm, n = 35) and much larger than the associated elliptical subsidiary caps (mmd 4.7μm ± 0.2 μm, n=40). Comparing the densities of these structures between the median and lateral areas (Table 1), it is apparent that in the former twice as many subsidiary caps are associated with each apical cap. This is largely a result of the greater number of apical caps in the lateral triangle which itself is probably due to a lack of pronounced valve sculpturing in this area. The presence of ocelli in the lateral triangle, therefore, does not appear to appreciably limit the distribution of apical caps. Ocelli are disposed in longitudinal rows radiating from the posterior jugal area, and aligned on the tegmentum in a manner corresponding to the position of the notches between insertion plates and sutural lamina in the articulamentum.

In the posterior valve, the mucro is depressed and terminal, and the sculpturing is similar to that of valves (II-VII) (Fig. 1(l)). This is reflected in the limited distribution of apical caps in the jugal and median areas (Table 1). Ocelli are infrequent and arranged in a lateral row along the mucronal ridge.

The ventral surface in all valves is rugose and unpolished with no slit rays apparent. In valve (I) the anterior margin is interrupted by 9 crenulate insertion plates. The adjacent eave tissue is perforated by large aesthete channels, however these do not extend to the ventral surface. In comparison the ventral surface of valves (II-VIII) are penetrated in the jugal area by large numbers of slit-like fissures resembling those found in *I. (I.) australis*. These valves are also perforated on the frontal and lateral edges between the tegmentum and articulamentum, and additionally in valve (VIII) on the posterior edge. Here, the growing edge is ventrally located, and hence aesthete channels open towards the anterior.



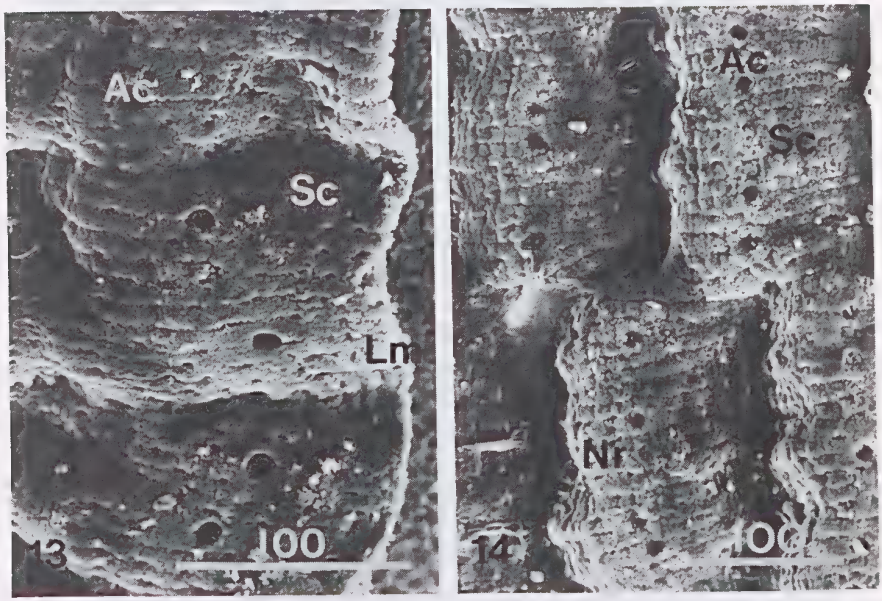


Figure 12. Anterior valve sculpturing in the lateral area of *L. (L.) gaimardi*, showing the ordered arrangement of subsidiary caps (Sc), and the distribution of apical caps (Ac) strictly limited to the central region of the raised nodules. Scale bar in micrometres.

Figure 13. Intermediate valve of *L. (L.) gaimardi,* showing the distribution of apical (Ac) and subsidiary caps (Sc) on the lateral margin (Lm) of the lateral triangle. Scale bar in micrometres.

Figure 14. Posterior valve of *L. (L.) gaimardi* in the antemucronal area, showing a dorsal sculpturing of nodulose ridges (Nr), and associated distribution of apical (Ac) and subsidiary caps (Sc). Scale bar in micrometres.

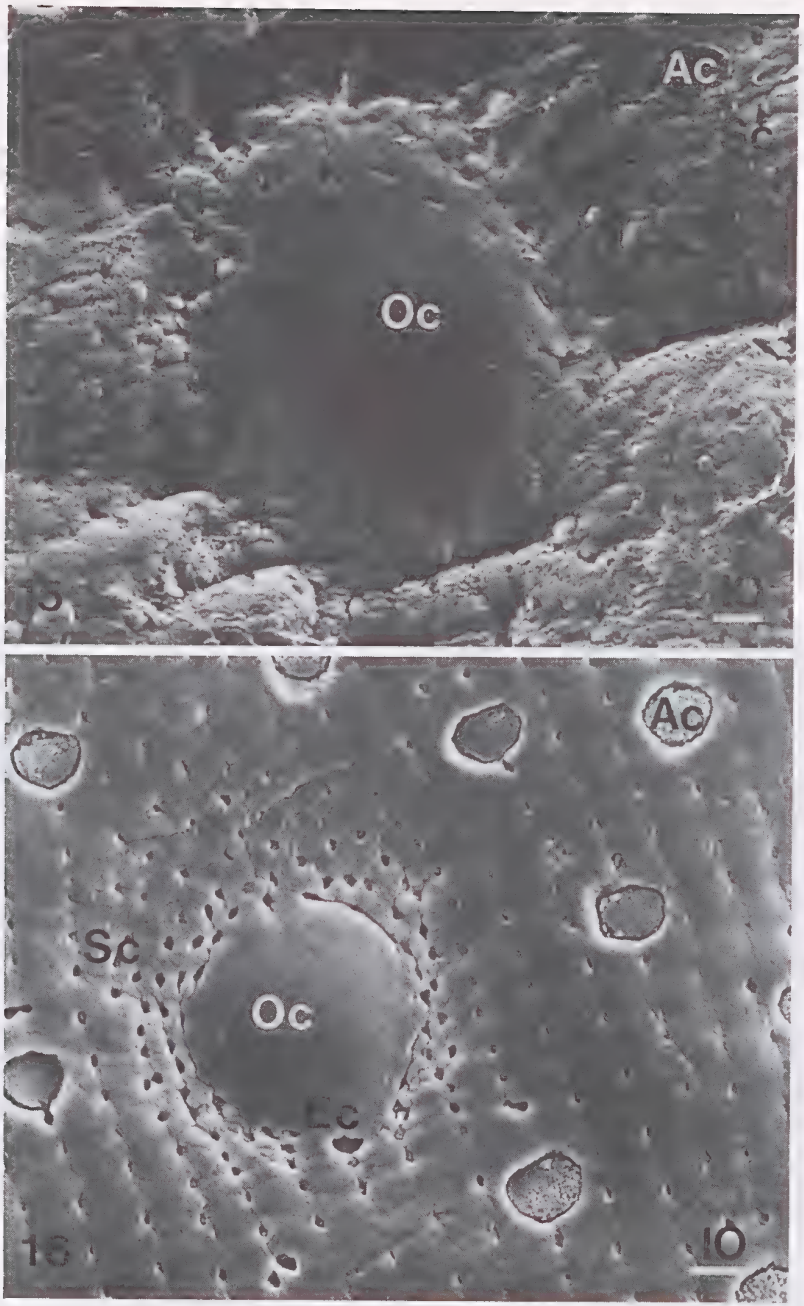


Figure 15. Dorsal surface of *L. (L.) gaimardi* near the frontal margin of an anterior valve, showing convex circular ocelli (Oc), and associated apical (Ac) and subsidiary caps (Sc). Scale bar in micrometres.

Figure 16. Dorsal surface of *O. quercinus* near the frontal margin of an anterior valve, showing a smooth convex ocellus (Oc) with its characteristic elliptical cap (Ec), surrounded by subsidiary (Sc) and apical caps (Ac). Scale bar in micrometres.

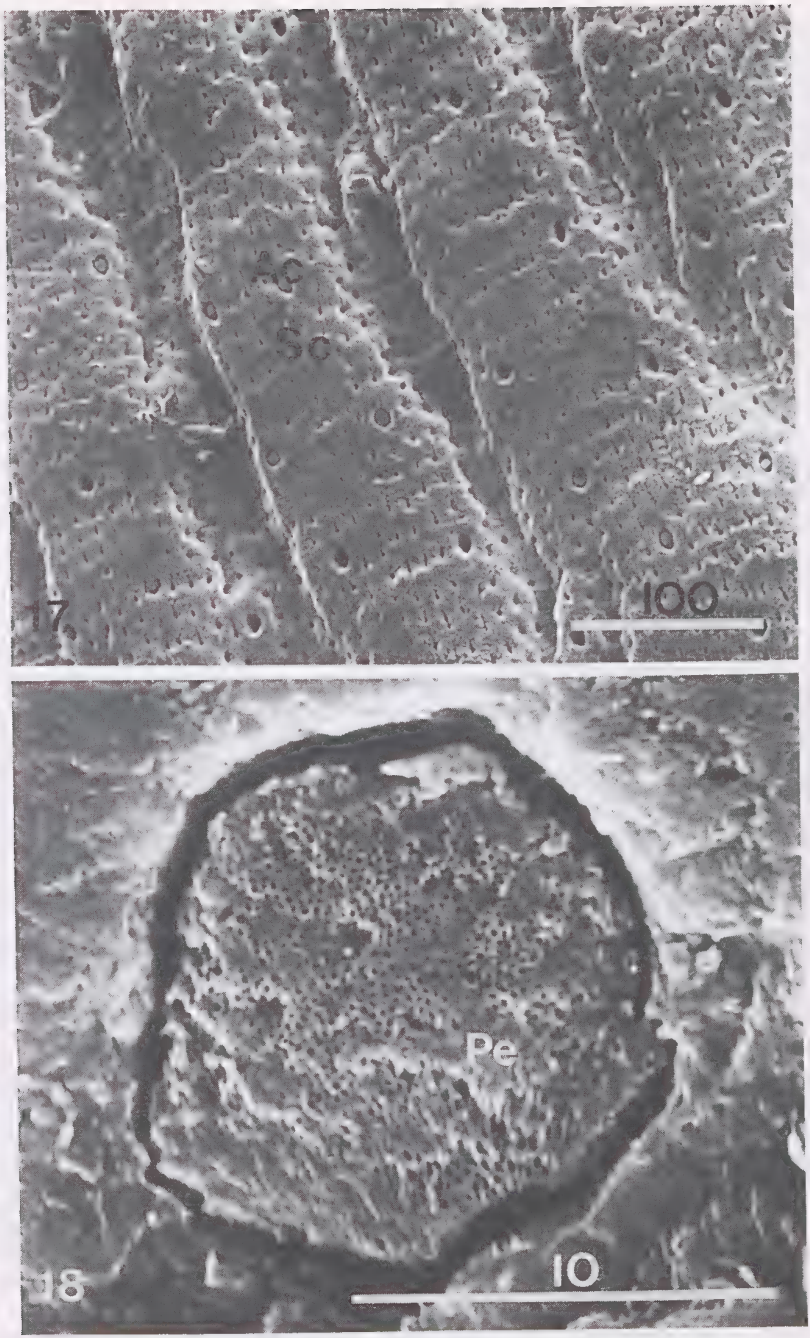


Figure 17. Intermediate valve of *O. quercinus* in the median area, showing the distribution of apical (Ac) and subsidiary caps (Sc) throughout the ribbed tegmentum. Scale bar in micrometres.

Figure 18. Apical cap on an intermediate valve of *C. mystica* treated with KOH to remove periostracum (Pe), revealing a perforated matrix beneath. Scale bar in micrometres.

Apical and subsidiary cap structure

The fine structure of the apical cap in all four species is similar. Each with a thin organic layer (or periostracum) covering the external surface. In older shell valves this layer is often partially or wholly absent revealing a honeycomb matrix beneath. When treated with KOH the apical caps are found to be perforated in an area that extends to the lateral regions of the cap (Fig. 18). These pores have a diameter of 150-200 nm and are separated by narrow spars (approximately 100 nm long).

The subsidiary caps in comparison were found to be unperforated, even after treatment with KOH.

DISCUSSION

Within a species the densities of both apical and subsidiary caps were found to vary not only between valves, but also between specific regions on valves. Baxter and Jones (1981) found that the shell valves of *Lepidochitona cinereus* (Linnaeus, 1767) were perforated by three distinct types of aesthete channels which might account for these differences. However, it appears that in the species examined in the present study, the variation in density is largely due to the dorsal valve sculpturing rather than aesthete channel differentiation.

Bullock (1985) suggested that apparent differences in aesthete cap density in the *Stenoplax limaciformis* (Sowerby, 1832) species complex, showed promise for phylogenetic studies. At present, the identification of a chiton species requires a combination of taxonomic characters including the number of slits on the insertion plates, the size, number and shape of girdle scales or spicules, and the radular structure (Iredale & Hull, 1927). The large number of taxonomic characters is necessary because of their considerable variability, both within and between populations. The use of cap densities as an additional taxonomic indicator would be advantageous if such a feature could improve consistency in taxonomic separations. As a result of the variation in cap densities between specific regions on individual shell valves, it is important that only cap densities from a given area of the shell valve be compared. Observations for the four species studied suggest that there is little intraspecific variation in density between posterior jugal areas of intermediate valves, where uneroded. If this proves consistent for other species of chitons, cap densities in posterior jugal areas could be an additional taxonomic character.

The classifications presented in Iredale & Hull (1927) and Kass & Van Belle (1980) consider Lepidopleuridae one of the most primitive families of the class Polyplacophora, Ischnochitonidae and Chitonidae as more advanced forms, and Acanthochitonidae and Cryptoplacidae as the most 'specialized' of the chiton families. Averages of cap densities for the total shell surface observed on each particular species in this study tentatively indicate a relationship between the phylogenetic status and the density of apical and subsidiary caps. *C. mystica*, belonging to the phylogenetically higher family of Cryptoplacidae, has a low average number (approximately 135/mm^2) of apical caps. In contrast, the more 'primitive' *I. (I.) australis* (Ischnochitonidae) has a much higher complement of apical caps (approximately 410/mm^2), whereas *L. (L.) gaimardi* and *O. quercinus* (both Chitonidae) have intermediate apical cap densities (approximately 172 and 349/mm^2 respectively). However, data for the jugal area of an intermediate valve of *C. achatinus* (Ischnochitonidae) presented by Baxter and Jones (1984), giving an

apical cap density of 112/mm², does not agree with the assumption that 'higher' families have smaller numbers of apical caps. Similarly, apical cap densities presented by Boyle (1974) for *L. cinereus* (Ischnochitonidae) indicate that low densities of apical caps occur in species belonging to more 'primitive' families. Subsidiary cap densities, likewise, do not reveal any phylogenetic trends. Further, examination of the apical/subsidiary cap ratios indicates extreme variation even within a family, for example valves (I) of the Chitonidae species *L. (L.) gaimardi* and *Onithochiton quercinus* have ratios of 1:28.0 and 1:17.1 respectively, whereas those of *Onithochiton neglectus* (Rochbrune, 1881) have approximately 1:7 (Boyle, 1976). Results recorded from the median areas of intermediate valves by Fischer & Renner (1979) give ratios of 1:13, 1:8 and 1:1-7 for *Chiton olivaceus* (Spengler) (Ischnochitonidae), *Lepidopleurus cajetanus* (Poli)(Lepidopleuridae), and *Acanthochitona fascicularis* (L.) (Acanthochitonidae), respectively. Hence the ratio of numbers of apical caps to subsidiary caps appears to be unrelated to the phylogenetic status of families (in the current classification systems), as are apical and subsidiary cap densities, and therefore it would appear unlikely that cap densities reflect evolutionary trends in Polyplacophora.

Although the function of aesthetes is far from clear, the periostracum secreting function proposed by Baxter *et al.* (1987) must be considered as one possibility. An erosion reducing secretion would certainly be advantageous to *L (L.) gaimardi* and *O. quercinus*, both of which are subject to considerable abrasion, unlike *I. (I.) australis* and *C. mystica*. Hence, the increased cap densities observed in the former species may reflect an evolutionary response to increased wave action.

Alternatively, aesthetes or specific aesthetes may function as photoreceptors. *I. (I.) australis* like *Chiton tuberculatus* (L.), (Arey & Crozier, 1919), shows a pronounced photonegative reaction to directed light (personal observations). In the field, *I. (I.) australis* is confined to gaps on the underside of large boulders during the day, becoming active and browsing at night. Hence, the behaviour pattern in this species may be largely determined by the aesthetes. *C. mystica* like *I. (I.) australis* is found on the underside of boulders, and does not display an obvious feeding cycle. *L. (L.) gaimardi* and *O. quercinus* in comparison are found on exposed open surfaces during the day, and like *I.(I.) australis*, exhibit a diurnal feeding cycle. Therefore, like *I. (I.) australis*, the cessation of daylight and hence stimulation of the aesthetes or ocelli (in *L. (L.) gaimardi* and *O. quercinus*), may act as a cue for nocturnal feeding excursions. I suggest that, in addition, the possible ability of a chiton to determine seasonal changes in day/night length by the aesthetes, may indicate that an important function of the aesthetes is to control gametogenesis. Photoperiod control of growth of gonads has been demonstrated in several species of sea stars, including *Pisaster ochraceus* (Brandt) by Pearse and Eernisse (1982) and *Asterias vulgaris* Verrill, by Pearse and Walker (1986). To date no such photoperiod experiments have been conducted with chitons, although Himmelman (1975) has considered photoperiod as a possible stimulus for spawning.

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LITERATURE CITED

Arey, L.B. & Crozier, W.J. 1919. The sensory responses of *Chiton*. J. Exp. Zool. 29: 157-260.

Baxter, J.M. & Jones, A.M. 1981. Valve structure and growth in the chiton *Lepidochitona cinereus* (Polyplacophora: Ischnochitonidae). J. Mar. Biol. Assoc. U.K. 61: 65-78.

Baxter, J.M. & Jones, A.M. 1984. The valve morphology of *Callochiton achatinus* (Mollusca: Polyplacophora: Ischnochitonidae). J. Zool. (Lond.). 202: 549-560.

Baxter, J.M., Jones, A.M. & Sturrock, M.G. 1987. The ultrastructure of aesthetes in *Tonicella marmorea* (Polyplacophora: Ischnochitonina) a new functional hypothesis. J. Zool. (Lond.). 211: 589-604.

Boyle, P.R. 1976. The aesthetes of chitons. III. Shell surface observations. Cell Tiss. Res. 172: 379-388.

Bullock, R.C. 1985. The *Stenoplax limaciformis* (Sowerby, 1832) species complex in the New World (Mollusca: Polyplacophora: Ischnochitonidae). Veliger. 27: 291-307.

Fischer, F.P. & Renner, M. 1979. SEM-Observations on the shell plates of three polyplacophorans (Mollusca: Amphineura). Spixiana. 2: 49-58.

Haas, W. 1972. Untersuchungen uber die mikro-und ultrastruktur der Polyplacophorenschale. Biomineralization. 5: 1-52.

Haas, W. 1977. Observations of the shell and mantle of the Placophora. In: The Mechanisms of Mineralization in invertebrates and plants. Wantabe, N. and Wilbur, K.M. (eds). Belle W. Baruch Libr. Mar. Sci. 5: 389-402.

Haas, W. & Kriesten, K. 1978. Die astheten mit intrapigmentatrum schalenauge von *Chiton marmoratus* L. (Mollusca: Placophora). Zoomorphologie. 90: 253-268.

Himmelman, J.H. 1975. Phytoplankton as a stimulus for spawning in three marine invertebrates. J. Exp. Mar. Biol. Ecol. 20: 199-214.

Iredale, T. & Hull, A.F.B. 1927. A monograph of the Australian Loricates (Phylum Mollusca Order Loricata). R. Zool. Soc. N.S.W. 1-168.

Kaas, P. & Van Belle, R.A. 1980. Catalogue of Living Chitons. Rotterdam, Backhuys. 144p.

Leloup, E. 1974. Quelques especes du genre *Onithochiton* Gray, 1847. Bull. Inst. R. Sci. Nat. Belg. 50(5): 1-17.

Moseley, H.N. 1885. On the presence of eyes in the shells of certain Chitonidae and on the structure of these organs. Quart. J. Microscop. Sci. 25: 37-60.

O'Neill, M.H.B. 1985. A review of the living New Zealand members of *Onithochiton* Gray, 1847 (Mollusca: Polyplacophora). N.Z. J. Zool. 12: 141-154.

Pearse, J.S. & Eernisse, D.J. 1982. Photoperiodic regulation of gametogenesis and gonadal growth in the sea star *Pisaster ochraceus*. Mar. Biol. 67: 121-125.

Pearse, J.S. & Walker, C.W. 1986. Photoperiodic regulation of gametogenesis in a North Atlantic sea star *Asterias vulgaris*. Int. J. Invert. Reprod. Dev. 9: 71-77.